The scaling effects of substrate texture on camouflage patterning in cuttlefish

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Abstract

Camouflage is the primary defense in cuttlefish. The rich repertoire of their body patterns can be categorized into three types: uniform, mottle, and disruptive. Several recent studies have characterized spatial features of substrates responsible for eliciting these body patterns on natural and artificial backgrounds. In the present study, we address the role of spatial scales of substrate texture in modulating the expression of camouflage body patterns in cuttlefish, *Sepia officinalis*. Substrate textures were white noise patterns first filtered into various octave-wide spatial frequency bands and then thresholded to generate binary (black/white) images. Substrate textures differed in spatial frequency but were identical in all other respects; this allowed us to examine the effects of spatial scale on body patterning. We found that as the spatial scale of substrate texture increased, cuttlefish body patterns changed from uniform, to mottle, to disruptive, as predicted from the camouflage mechanism of background matching. For substrates with spatial scales larger than skin patterning components, cuttlefish showed reduced disruptive patterning. These results are consistent with the idea that the body pattern deployed by a cuttlefish attempts to match the energy spectrum of the substrate, and underscore recent reports suggesting that substrate spatial scale is a key determinant of body patterning responses in cuttlefish.

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1. Introduction

Cephalopod camouflage is among the most sophisticated in the animal kingdom because the neurally controlled chromatophores permit a diverse repertoire of body patterning that can be changed in milliseconds (Hanlon, 2007; Hanlon & Messenger, 1988; Messenger, 2001). Cuttlefish (Sepioidea: Cephalopoda) use two distinct camouflage tactics – background matching and disruptive coloration (Cott, 1940) – to conceal themselves on various backgrounds (Hanlon, 2007; Hanlon and Messenger, 1996). In background matching, the animal's appearance generally matches the color, lightness and pattern of one or several areas of the background (Endler, 1978, 1984; Stevens & Merilaita, 2009a). In disruptive coloration, the animal's appearance is disrupted by strongly contrasting patterns that break up the body outline, thus reducing visual recognition by the predators (e.g., Cott, 1940; Edmunds, 1974; Stevens & Merilaita, 2009b; Thayer, 1909), yet disruptive patterns also provide some aspects of background matching (Endler, 1978; Fraser, Callahan, Klassen, & Sherratt, 2007; Hanlon et al., 2009; Stevens, Cuthill, Windsor, & Walker, 2006). Although there are numerous variations in the details of the body patterns shown by cuttlefish for camouflage, all skin coloration patterns can be grouped into three pattern types: (1) uniform (or uniformly stippled), (2) mottle, and (3) disruptive; the first two types contribute to background matching, and the third one is a form of disruptive coloration (Hanlon, 2007; Hanlon & Messenger, 1988; Hanlon et al., 2009).

The expression of camouflage body patterns in cuttlefish is a visually driven behavior (Hanlon & Messenger, 1988; Holmes, 1940; Marshall & Messenger, 1996), and previous studies have shown that certain background variables, such as brightness, contrast, global configuration, edge and size of objects are essential for eliciting these body pattern types (Barbosa, Litman, & Hanlon, 2008; Barbosa et al., 2007; Barbosa, Mathger et al., 2008; Chiao, Chubb, & Hanlon, 2007; Chiao & Hanlon, 2001a, b; Chiao, Kelman, & Hanlon, 2005; Kelman, Baddeley, Shohet, & Osorio, 2007; Kelman, Osorio, & Baddeley, 2008; Mathger, Barbosa, Miner, & Hanlon, 2006; Mathger et al., 2007; Shohet, Baddeley, Anderson, Kelman, & Osorio, 2006; Shohet, Baddeley, Anderson, & Osorio, 2007; Zylinski, Osorio, & Shohet, 2009). Among these visual features, the size (or scale) of background patterns deserves special attention. Earlier work using checkerboard backgrounds has shown that check sizes roughly 40–120% of white square (WS) area (a salient skin component on the cuttlefish mantle with an area approximately 10% of the overall size of the animal; see Fig. 1) can evoke disruptive body patterns in cuttlefish (Barbosa et al., 2007; Barbosa, Mathger et al., 2008; Chiao & Hanlon, 2001a; Chiao et al., 2007; Kelman et al., 2007, 2008; Mathger et al., 2006), while smaller check sizes near 4–12% of WS area are likely to elicit mottle patterns, and larger check sizes around 400–1200% of WS area make most animals express uniform body patterns (Barbosa et al., 2007; Barbosa, Mäthger et al., 2008; Zylinski et al., 2009).

These results suggest that body patterning of cuttlefish is scale dependent; however, checkerboards are a very restricted class of images. Moreover, checkerboards might well be a special class for cuttlefish, given that the primary constituent elements of checkerboards (square checks) match the form of the single most salient disruptive component in the cuttlefish repertoire (the white square in the middle of its dorsum). The purpose of the current experiment is to see whether the scale-dependency of the cuttlefish patterning responses previously observed with checkerboards generalizes to other substrates.

That such scale-dependency may well be a primary visual background sampling rule is suggested by Fig. 1. This image contains two cuttlefish (one in center, another in lower-right),

each deploying a strongly disruptive response pattern. The background of this image comprises many high-contrast elements, large in size in comparison to the two animals and to the disruptive components in their patterning repertoires. Although no single element in the background pattern is a good size match to the white square of the more central cuttlefish, this white square is highly activated. Responses like this suggest that the overall scale and contrast of the background may be equally or more important in evoking disruptive response patterns than the resemblance of elements in the background to specific disruptive components available to the cuttlefish.

Fig. 1. Cuttlefish, *Sepia officinalis*, on crushed oyster shells. Two juvenile cuttlefish show strong (center one) and weak (lower-right corner) disruptive body patterns to conceal themselves on natural substrates. Note that several salient disruptive components (i.e., white square and white head bar, see text for details) do not resemble in size any object in this picture, yet both animals camouflage well on this background.

To study the dependency of cuttlefish response patterns to spatial scale, we created random background textures (very different from checkerboards) differing in scale but identical in all other respects (see Fig. 2). These texture substrates were derived by filtering white noise patterns into isotropic, octave-wide frequency bands and thresholding at zero to yield binary patterns with equal numbers of black and white pixels (see Section 2). To objectively quantify the disruptive body patterns of cuttlefish on substrates of different scales, we also developed a new set of statistics to estimate the disruptive scores. In general, our results support the concept that the cuttlefish patterning responses depend on substrate spatial scale. We discuss the scale-dependency in the context of cuttlefish camouflage tactics.

2. Materials and methods

2.1. Animals and experimental setup

Fifteen cuttlefish (*Sepia officinalis*), ranging in size between 3.3 and 4.9 cm mantle length (ML), were used in this study. All animals were hatched, reared, and maintained at the MBL Marine Resources Center (Woods Hole, MA). To provide a stable visual environment and minimize stress to the animals, the experimental trials were conducted inside a tent made of black plastic sheeting. Each animal was placed in a tank (55 cm × 40 cm × 15 cm) with

flowing seawater and restricted to a cylindrical arena (25 cm diameter, 11 cm height) where various computer-generated texture substrates (laminated to be waterproof) were presented on both the floor and wall. To reduce repeatedly transferring animals between the holding tank and experimenting arena, each animal was tested on 3–4 different substrates in a random order, with at least 30 min between treatments. A circular 40 W fluorescent light source (Phillips CoolWhite) was used to reduce the effect of shadow. A light meter (Extech EasyView EA30) was used to take readings around the perimeter and near the center of the arena (center 1.07 klux; perimeter 1.03 klux), showing that the arena was lit relatively evenly. Once the animal had acclimated (i.e., ceased swimming and hovering movements and expressed a stable body pattern), three still images were taken at 4 min interval using a digital video camera (Panasonic PVGS400) mounted 60 cm above the arena and connected to an external monitor so that the animal's movements could be followed from outside the chamber without disturbing it. The three images per animal per substrate in each trial were used to quantify the animal's response (see Section 2.4).

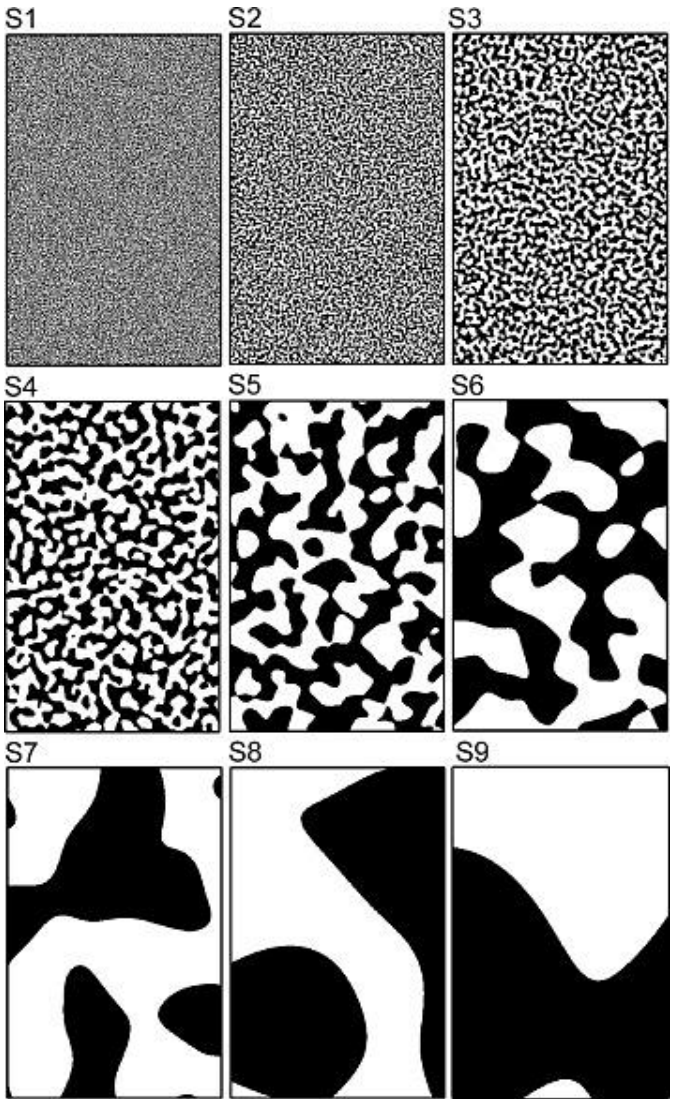

Fig. 2. Nine scales of substrate textures used in the present study. Each substrate is a binarized bandpass-filtered image of a random noise. From S1 to S9, the size of the band-pass filter increases in an octave fashion. This series of substrate textures has equal contrast and intensity, differs only in spatial scale. They can be thought as the same substrate viewed from different distances.

2.2. Substrates

Substrates were generated by band-pass filtering spatial white noise into nine, octave-wide, isotropic, spatial frequency bands (filter impulse responses were zero-mean, differences-of-circular-Gaussians) and then thresholding the resulting filtered noise images at zero. This yielded substrates with roughly equal numbers of black and white pixels. These nine binary images have the general appearance of Holstein cow patterns (Fig. 2). From S1 to S9, each successive substrate has double the scale of the preceding one. Thus, substrate S2 has scale twice that of S1; S3 has scale twice that of S2, and so forth.

2.3. Quantification of the strength of disruptive coloration

We developed an automated method to quantify the activation of five light and five dark skin components responsible for disruptive coloration previously described in *S. officinalis* (Hanlon & Messenger, 1988). To perform this component analysis, each animal image was first cut out from the background on which it appears and warped to conform in size and shape to a standard cuttlefish template. The green[1] "landmark lines" in Fig. 3A–C were all derived from points supplied by the user through mouse clicks on the original cuttlefish image for use in warping the cuttlefish image to the standard image. Then three intensity traces were extracted from the image: the medial trace, the transverse mantle trace and the transverse head trace. The medial trace (blue line, Fig. 3A) gives the fluctuation in image contrast ([intensity - (image mean)]/(image mean)) as a function of distance along the red lines in Fig. 3A from the topmost to the bottommost point. (This trace is actually the slightly smoothed average of the traces derived from the three parallel red lines in Fig. 3A.) Similarly, the transverse mantle and transverse head traces give the fluctuation in image intensity along the red lines in Fig. 3B and C as one moves from left to right. Seven statistics derived from the medial trace were used to estimate the activation strengths of three light components (WHB, white head bar; WS, white square; WPT, white posterior triangle) and four dark components (AHB, anterior head bar; AMB, anterior mantle bar; ATML, anterior transverse mantle line; PTML, posterior transverse mantle line). Activations of AHB, WHB, ATML, and PTML were derived from the extreme values of particular peaks or troughs (identified with reference to the green landmark points) in the medial trace, whereas activations of AMB, WS, and WPT were estimated by averaging the trace within given regions. In similar fashion, the activation strengths of one light component (WMB, white mantle bar) and one dark component (MMS, medial mantle stripe) were extracted from the transverse mantle trace. (The estimate of the WMB (MMS) activation was derived from averaging two WMB (MMS) estimates on the left and right sides of the mantle.) Finally, the activation strength of one light component, the white arm triangle (WAT), was derived from the transverse head trace.

An overall summary statistic reflecting strength of disruptive responding was then derived from the 10 component activation strengths of each cuttlefish. The aim of this summary statistic was to approximate a manual scoring method used in previous research (Barbosa et al., 2007; Barbosa, Mäthger et al., 2008; Chiao et al., 2007; Mathger et al., 2006, 2007). To derive the summary statistic used here, we (1) chose 40 images of representative body patterns (ranging from highly disruptive to uniform), (2) scored each image manually

[1] Please note that Figs. 1, 3, and 7 will appear in B/W in print and color in the web version. Based on this, please approve the footnote 1 which explains this.

using the previously described grading scheme (Mäthger et al., 2006), and (3) used the automated method described above to derive a vector of 10 component scores from each image. We then used standard linear regression to derive a linear combination of the 10 activation strengths to optimally (in a least-squares sense) predict the 40 manual scores (see supplementary Figure S1 for correlation between manual scores and predicted scores).

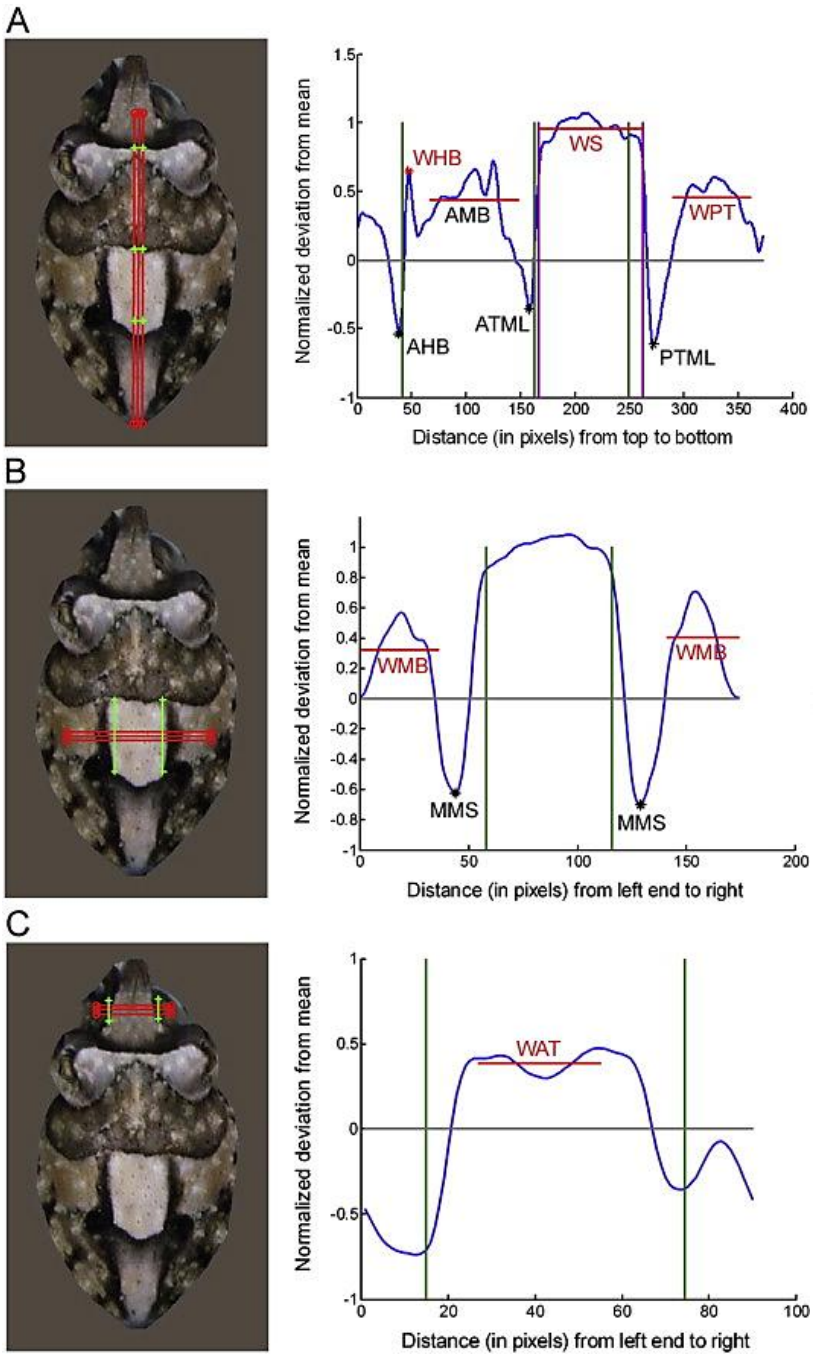

Fig. 3. Activation of 10 disruptive components can be estimated from the intensity profiles along main body axes. To extract the expression levels of five light and five dark skin components previously identified in *S. officinalis* (Hanlon & Messenger, 1988), the pixel intensity profiles along one medial line and two transverse lines (head and mantle) were used to estimate their activations. (A) Three light components (WHB, white head bar; WS, white square; WPT, white posterior triangle) and four dark components (AHB, anterior head bar; AMB, anterior mantle bar; ATML, anterior transverse mantle line; PTML, posterior transverse mantle line) are derived from the intensity trace of the medial line. We sample image intensities along the three red lines and take the average of the three traces. (B) One light component (WMB, white mantle bar) and one dark component (MMS, medial mantle stripe) are calculated by averaging activations derived from the intensity trace of a line that runs horizontally across the region of the WS. (C) The light component on the head (WAT, white arm triangle) is estimated from the intensity trace of a line that runs horizontally across the head region.

2.4. Quantification of body patterns

We also developed an automated method to characterize the pattern produced by an animal that would enable us to discriminate between uniform/stipple, mottle and disruptive

patterns (see Barbosa, Mäthger et al., 2008 for details). Disruptive patterns are marked by large-scale, bright and dark components of multiple shapes and orientations, whereas mottle patterns are marked by fine-grained light/dark variations, and uniform/stipple patterns are even finer in texture (Hanlon et al., 2009). In other words, these three pattern types differ in granularity (or spatial scales). We can capture such differences by analyzing the image of the animal in different spatial frequency bands. Similar to the skin component analysis described above, each animal image was cut out from its context and warped to conform in size and shape to a standard cuttlefish template. Six octave-wide isotropic ideal filters were used for this granularity analysis. Applying these six filters to the warped cuttlefish image yielded six images that partition the information in the original image into different "granularity bands" (discarding a small amount of information in the highest frequencies). Our use of octave-wide frequency bands was motivated by the following considerations: as observed by Field (1987), natural images have (roughly speaking) the property that their energy spectra are invariant with respect to viewing distance. This immediately implies that all octave-wide frequency bands must (on average) contribute equal energy to natural images because any octave-wide frequency band in a natural image can be converted into any other by an appropriate change in viewing distance. Thus, deviations from uniformity in the granularity spectrum reflect strategic patterning that deviates from what one might expect by default from a patch of natural image.

From each of the six band-pass filtered images, we extracted one number: the sum of the squared pixel values in that image. This is the total energy of the original, standardized image in the given spatial frequency band. We refer to these six energies as the "granularity spectrum" of the image. The scale of these numbers is arbitrary. We use a scheme in which energy is expressed as a mean quantity per pixel and is normalized to reflect a proportion of the maximum possible energy that could exist in any image (note: the images have pixel values of 0–255). This energy measure is closely related to the root-mean-square (RMS) contrast typically used in characterizing the contrast of complex scenes (Bex & Makous, 2002); specifically, the square root of the sum of the granularity spectrum values would closely approximate the RMS energy in the image. Based on the shape of this granularity spectrum, three major body patterns (uniform/stipple, mottle, and disruptive patterns) can be readily distinguished. Typically, the spectrum of the uniform/stipple response has low energy in all six granularity bands. The mottle pattern yields a spectrum with more energy at all bands than the uniform/stipple pattern, and this spectrum has highest energy in granularity bands 3 and 4, which are by definition mid scale in size. Finally, the disruptive pattern evokes a spectrum with more total energy than either the uniform/stipple or mottle patterns, and most of this energy is in the two coarsest (i.e., large scale) granularity bands 1 and 2.

To further characterize the granularity spectrum of each body pattern described above, two additional statistics (TE and MG) were derived to quantify the magnitude and shape, respectively, of the granularity spectrum (Barbosa, Mäthger et al., 2008). The *total spectrum energy* (TE) was computed by adding together the six granularity spectrum values. This reflects the overall amplitude of the spectrum. This statistic essentially gauges the overall contrast of the pattern expressed by the animal. The *spectrum mean granularity* (MG), on the other hand, was defined as:

$$MG = \frac{\sum_{g=1}^{6} gS(g)}{TE}$$

where g is the energy band number in the granularity spectrum, and $S(g)$ is the strength in

each granularity band (i.e., the granularity spectrum value). This measure is likely to reveal systematic changes in spectrum shape. The higher the MG, the finer (i.e., smaller scale) the corresponding cuttlefish body pattern will tend to appear. Thus, this statistic essentially gauges the overall granularity of the body pattern expressed by the animal.

3. Results

3.1. Disruptive body patterns of cuttlefish can be influenced by substrate scale

Fig. 4 shows representative cuttlefish body pattern responses on each of nine substrates (S1–S9). Animals typically showed uniform/stipple patterns on the smallest scale substrate (S1), and exhibited mottle patterns on S2. Cuttlefish usually had a mixed response of mottle and weak disruptive patterns on S3. From S4 to S6, cuttlefish consistently expressed strong disruptive patterns. Although most animals still showed moderate disruptive responses on S7 and S8, a few animals reduced their disruptive body patterning (i.e., they showed fewer of the 11 disruptive skin components from which disruptive patterns are made up; see Hanlon & Messenger, 1988). The individual variation in body patterns was most obvious when cuttlefish were tested on S9.

Using the automated grading method, we calculated the average summary disruptive score (across the three images taken) for each animal on each substrate. Fig. 5 shows averaged summary disruptive scores for 15 animals across nine substrates ($F_{8,112} = 14.493$, $p < 0.01$). From S1 to S3, although disruptive responses appear to increase slightly, these differences are not significant. However, from S3 to S4, the doubling of spatial scale in substrate texture produced a significant increase in disruptive scores ($p < 0.01$, *post-hoc* test of pairwise comparison from the repeated-measures ANOVA, significance is Bonferroni adjusted). Generally, cuttlefish showed the strongest disruptive body patterns on S5 and S6 with disruptive scores tending to decrease from S7 to S9. The coarsest (i.e., largest scale) substrate texture (S9) evoked summary disruptive scores that were comparable on average to those evoked by S3; however, response variation was greater on S9, and the composition of disruptive components expressed was different on two substrates (see S3 and S9 in Fig. 4).

A more detailed look at the cuttlefish's body patterning responses is given in Fig. 6. Each panel shows the activation of one disruptive skin component evoked by all nine substrates in all 15 animals. Take the upper left panel, for example. Each of the thin lines in this panel plots the activation of the white posterior triangle (WPT) evoked in a single cuttlefish by substrates S1–S9. The thick black line in each panel gives the mean (across all animals) activation produced in the given skin component by each substrate. The main impression produced by these plots is that the animals tend to vary widely in their responses to most of these substrates. Different cuttlefish show different response proclivities (note: an ANOVA analysis with subjects as a variable showed no significant individual difference for the majority of disruptive components); that is, the fine-tuning of the body pattern can vary but the choice of the overall body pattern template (in this case, disruptive) is similar in all animals on any given substrate. However, there are some important general trends.

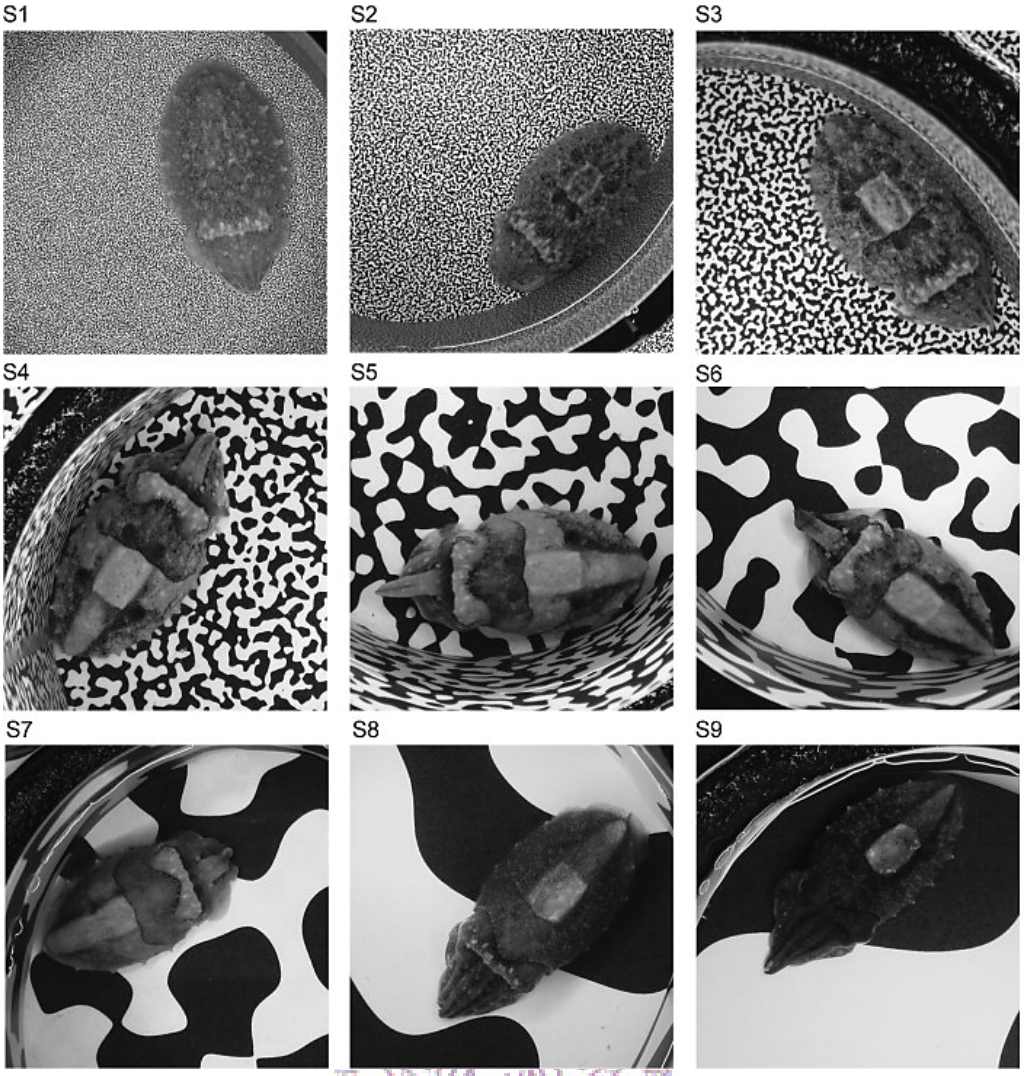

Fig. 4. Representative body patterns of cuttlefish on various sizes of substrate texture. Background textures (S1–S9) are identical to those shown in Fig. 2. Animals showed a transition from uniform/stipple and mottle patterns to disruptive patterns as the substrate scale increases. However, cuttlefish did not return to uniform patterns on the last few textures (S7–S9); rather they only showed weakened disruptive body patterning.

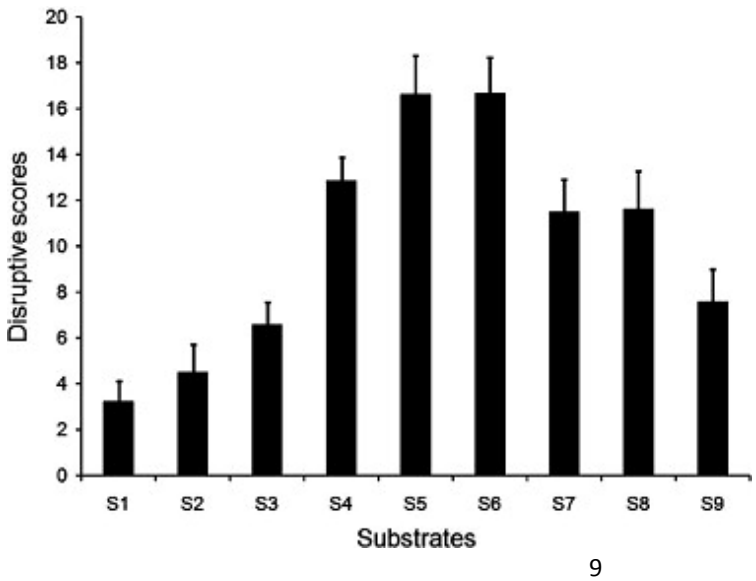

Fig. 5. Disruptive scores of cuttlefish depend on substrate scale. Animals show increasing disruptive coloration from S1 to S6, but the strength of disruptive body patterning decreases in S7–S9 ($n = 15$). The data are mean ± sem.

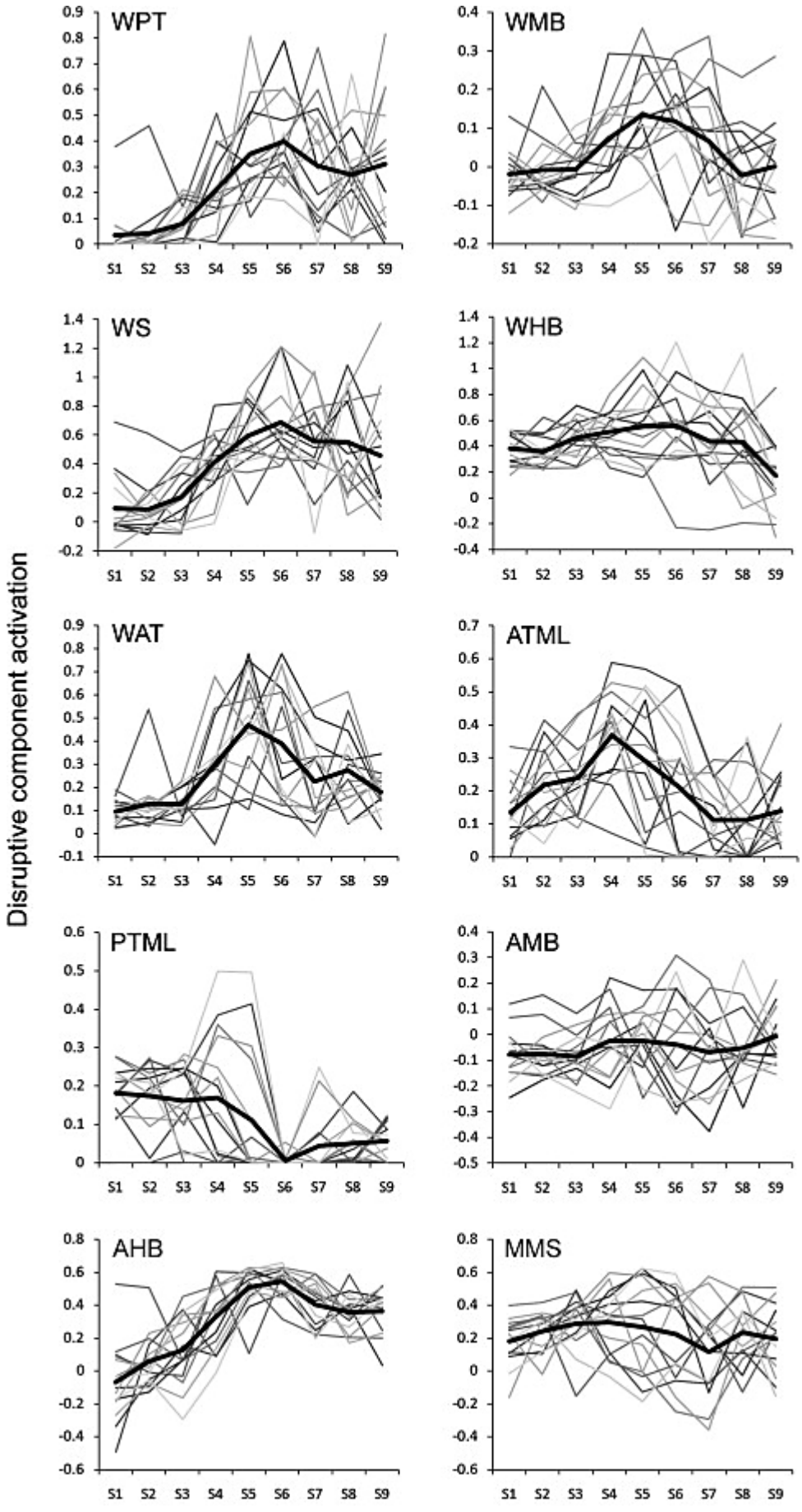
WPT
WMB
WS
WHB
WAT
ATML
PTML
AMB
AHB
MMS
S1 S2 S3 S4 S5 S6 S7 S8 S9
Disruptive component activation
Substrates

Fig. 6. Activations of individual disruptive components evoked by different substrates. Each panel shows the activation of one disruptive skin component evoked by all nine substrates in all 15 animals. Each of the thin lines in panel one, for example, plots the activation of the white posterior triangle (WPT) evoked in a single cuttlefish by substrates S1–S9. The thick black line in each panel gives the mean (across all animals) activation produced in the given skin component by each substrate. Each of the five components whose data are plotted in the left column shows statistically significant, systematic variation across substrates. The components whose data are plotted in the right column show no significant effects.

Repeated measures ANOVAs reveal that each of the five components whose data are plotted in the left column of Fig. 6 shows significant, systematic variation across substrates (WPT, $F_{8,112} = 21.516$; WS,$F_{8,112} = 12.120$; WAT, $F_{8,112} = 9.110$; PTML, $F_{8,112} = 8.919$; AHB, $F_{8,112} = 12.395$; $p < 0.01$). The components whose data are plotted in the right column show no significant effects (WMB, $F_{8,112} = 3.217$; WHB, $F_{8,112} = 5.039$; ATML, $F_{8,112} = 5.378$; AMB, $F_{8,112} = 0.856$; MMS, $F_{8,112} = 0.396$; $p > 0.05$). When we focus just on the skin components shown in the left column, we note that the average trends (shown by the thick black lines) are similar for the white posterior triangle (WPT), the white square (WS), the white arm triangle (WAT) and the anterior head bar (AHB). For each of these skin components the pattern closely parallels that shown by the summary disruptive statistic plotted in Fig. 5: activation tends to increase, reaching a maximum at substrate S5 or S6, and then decreases.

The only skin component that does not fit this trend (i.e., activation monotonically increased and reached a maximum at substrate S5 or S6, then gradually decreased) is the posterior transverse mantle line (PTML), whose activations seem to run contrary to the usual trend seen in the other four skin components. A close look at the patterns produced by cuttlefish reveals why this is so. The PTML is a dark skin component at the rear of the white square. Deployment of this component serves to accentuate the white square as a singular visual element of the scene. It is strongly activated, for example, in the highly disruptive response shown by the animal in Fig. 3, producing a salient edge between the white square and the region of the white posterior triangle. Compare this pattern to that shown by the animal in Fig. 4 on substrate S7. In the latter animal, the PTML is completely absent, yet we would nonetheless classify the pattern shown by this animal as strongly disruptive. Moreover, the tactic of this animal's body patterning is clear: by suppressing activation of the PTML, this animal combines its white square and white posterior triangle into a single, elongated white mass that seems to match (in width and degree of elongation) some of the light features of the substrate S7.

It is a striking aspect of our data that all animals suppress PTML activation almost completely on substrate S6. The reason, we speculate, is that S6 comprises many regions that are both elongated and approximately equal in width to the combination of the white square and white posterior triangle. Our speculations suggest that we might observe more activation of the PTML if these same cuttlefish were placed on a checkerboard of comparable spatial scale to S6; this awaits empirical investigation.

3.2. Body patterning of cuttlefish is largely substrate-scale dependent

While disruptive scores of cuttlefish are modulated by the spatial scale of substrate texture, this measure alone does not specify the body patterns that animals show on a given substrate. To evaluate the appearance of cuttlefish body patterning, we computed granularity

spectra for each animal on nine substrates (see supplementary Figure S2 for granularity analysis of these substrate textures). Fig. 7A shows averaged granularity profiles of body patterns for all substrates (S1–S9). Not only did cuttlefish express typical stipple/mottle granularity spectra on S1–S3, but the overall energies for animals on S1–S3 were also much lower than on the other six substrates (S4–S9), with the total energy increasing monotonically from S1 to S3 (Fig. 7B). These three granularity spectra indicate that body patterns of cuttlefish on S1–S3 are dominated by small-scale components on the skin, rather than by large-scale chromatic components (Fig. 7C), and review of the photographs of these animals' body patterns confirms this. Considering the small scale of these substrate textures, this is suggestive of background matching in terms of spatial scale match between animal and background. In comparison, from S4 to S9, animals showed increased energy in granularity bands 1 and 2 (Fig. 7A), an indication of increasing recruitment into the skin of larger disruptive components of the body patterns. As previously observed, highly disruptive patterns typically yield high total energy (sum of the six granularity energies); thus, given that S5 and S6 evoked the highest summary disruptive scores (see Fig. 5), we might expect them to yield the highest total energy. This is the case as seen from Fig. 7B. It is also evident in Fig. 7B that total response energy tends to decrease on S8 and S9 suggesting that disruptive body patterning is reduced when substrate scale is beyond the size of animal body.

4. Discussion

For animals with adaptive camouflage capabilities that are mediated by visual perception of background features, spatial scale of background is commonly assumed to play a major role in determining spatial scale of animal body patterns to achieve background matching (Endler, 1984; Stevens and Merilaita, 2009a), but direct evidence to support this assumption is lacking. By carefully designing substrate texture, in which only the spatial scale was systematically modulated and other spatial properties remained unchanged, we show here that body patterning of cuttlefish (*S. officinalis*) is highly dependent of spatial scale of background.

Previous studies have shown that size (or area) of discrete light objects on a dark background is crucial for evoking disruptive body patterns in cuttlefish (Barbosa et al., 2007; Barbosa, Mäthger et al., 2008; Chiao and Hanlon, 2001a, 2001b; Chiao et al., 2007; Mäthger et al., 2006; Mäthger et al.; 2007 and Shohet et al., 2007). Specifically, when the size (or area) of light objects is roughly equal to the area of white square (WS) component on the mantle and the background is generally dark, then disruptive body patterns are expressed by cuttlefish. This visual sampling rule for disruptive body patterning has been well established (Hanlon, 2007). However, based on the results from the present study, we can now expand our previous visual sampling rule to include non-discrete objects, or more specifically, to emphasize that the scale of substrate texture (not merely the size of discrete objects) is also a powerful determinant of cuttlefish body pattern responses.

The overall patterns in the data conformed to expectations. As the substrate scale was increased from fine to coarse, the cuttlefish body patterns also changed in coarseness from uniform/stipple to mottle to disruptive. As the scale of the background pattern was increased beyond that of the cuttlefish disruptive skin components, the animals began to show uniformly light or dark body patterns with a few disruptive components being expressed.

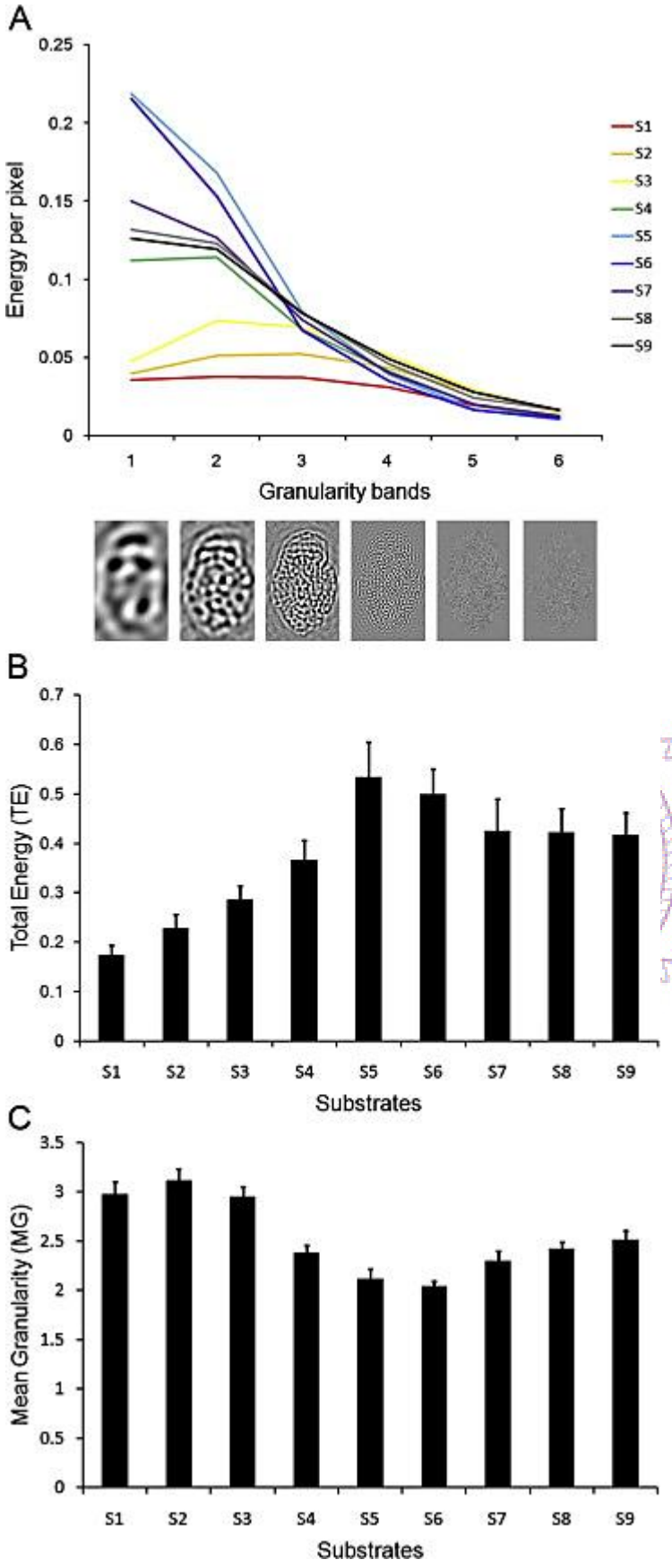

Fig. 7. Granularity profiles of body patterning depend on substrate scale. (A) Cuttlefish express typical stipple/mottle granularity profiles on S1–S3. From S4 through S9, animals show higher energy in granularity bands 1 and 2, a signature of disruptive body patterns. Notably, animals on S5 and S6 have the highest energy per pixel in granularity statistics, which correspond well with the highest disruptive scores in Fig. 5. Represented images of six granularity bands are shown below the plot to illustrate the relative scales. The data is granularity averaged from 15 animals. Error bars are not shown for clarity. (B) Average total energies (TEs) of granularity spectra of all animals on nine substrates were plotted to indicate that body patterning strength (contrast) is dependent of substrate scale. (C) Average mean granularities (MGs) of animals on all substrates were shown to suggest that body patterning component size is correlated with the substrate spatial scale. The error bars in (B) and (C) represent SEMs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Some curious trends are noteworthy. First, animals showed significantly higher levels of disruptive responses on substrate S3 than on S1 and S2 (a paired comparison *t*-test comparing summary disruptive response strength on S3 with the mean disruptive response strength on S1 and S2 yielded $p < 0.009$, paired $t(14) = 3.04$), and disruptive responses on S4 were substantially higher still (See Fig. 5). However, the scales of substrates S3 and S4 are much finer than the disruptive skin components prominently activated by these substrates. Notice, for example, the response of the animals in Fig. 4 on substrates S3 and S4. Both animals show strong activation of the white square despite neither substrate having any blobs comparable in size to the white square. The scale of S3 and S4 would seem to dictate mottle rather than disruptive body pattern responses. In addition, we note fairly high levels of disruptive component expression on substrates S8 and S9 even though the light and dark elements of these two substrates are all much larger in scale than the cuttlefish disruptive skin components. Given that the components of substrates S8 and S9 are comparable to or larger in size than the entire body of the cuttlefish, one might have expected animals to adopt uniform coloration on these coarser substrates to achieve background matching. We see then that animals commonly deploy disruptive body patterns on substrates to which those patterns are mismatched in scale. This suggests that one tactical aim of disruptive coloration is distinct from background matching. In a recent experiment, however, Kelman et al. (2007) demonstrated that edge information is required for cuttlefish to deploy disruptive body patterns (note that the contrast energy between the checkerboards and phase-randomized checkerboards in their experiment was also different, thus making it difficult to ensure the importance of edge information in evoking disruptive coloration), and they concluded that disruptive coloration is used when it allows general background matching to the surroundings. Furthermore, Zylinski et al. (2009) recently showed that even isolated edges (without contiguous objects) are sufficient to elicit some disruptive components of body patterns, and argued that intermediate expression of disruptive components (what we might term weak disruptive patterns with only a few disruptive components being expressed) is a mechanism of background matching. Whether disruptive camouflage can be distinguished as a distinctive visual camouflage mechanism from background matching in cuttlefish remains an open question (Hanlon et al., 2009). This general subject is under scrutiny by many biologists currently studying camouflage mechanisms (Endler, 2006; Fraser et al., 2007; Kelman et al., 2007; Merilaita & Lind, 2005; Schaefer & Stobbe, 2006; Stevens, Cuthill, Alejandro Parraga, & Troscianko, 2006; Stevens & Merilaita, 2009b).

One of the main camouflage tactics used throughout the animal kingdom is background matching, in which animals achieve concealment by “matching” their body patterns to the substrate textures (Endler, 1978, 1984; Stevens and Merilaita, 2009a). Indeed, it has been argued that *all* cuttlefish response patterns have some degree of background matching; uniform and mottle body patterns have a high degree of general resemblance to the background, and Disruptive patterns not only disrupt the recognizable body outline but also provide at least a moderate degree of background matching (Hanlon and Messenger, 1996; Hanlon et al., 2009). The deployment of disruptive patterning by animals on substrates S3, S4–S8 and S9 is an interesting finding, and how it fits in with the overall camouflaging mechanisms of cuttlefish requires future experimentation.

4.1. Is disruptive body coloration an alternative form of background matching?

It is noteworthy that substrates in these experiments are all extremely high in contrast, higher than any the animals will encounter in their natural habitat. Indeed, it is physically

impossible for cuttlefish to achieve body patterns comparable in contrast to these substrates (to do so, they would have to make every skin component on their bodies either white or black). It seems highly likely that substrate contrast (as reflected by the standard deviation of substrate intensity histogram) is a crucial statistic for the animal to match when it strives for general background matching. It is known, for example, that human observers are highly sensitive to spatial variations in this statistic (e.g., Chubb, Nam, Bindman, & Sperling, 2007); thus, human predators would be very likely to detect a target that differed substantially from its background in this statistic. Many animals also have refined contrast perception. It is also true, however, that among the response options available to the cuttlefish, disruptive patterns are higher in physical contrast than either uniform or mottle responses. Thus, for background matching (i.e., mottle and uniform body patterns), it is a biological imperative for animals to try to match the contrast of their body pattern to the contrast of the substrate, and we should expect them to be highly biased to produce high-contrast disruptive responses in the current experiment, even on substrates mismatched in scale to their disruptive skin components. This line of thought receives further support from experiments using checkerboard substrates in which it has been found that increasing the contrast of a checkerboard substrate of any given scale tends to increase disruptive responding (Barbosa, Mäthger et al., 2008), again suggesting that animals may sacrifice a match in pattern granularity for the sake of equating their body pattern to the background in contrast. Furthermore, in a separate experiment, we also found that reducing contrast of these texture substrates would tend to decrease their disruptive responses (Hanlon et al., 2009). In addition, our previous study showed that cuttlefish are able to perceive objects in their background differing in contrast by approximately 15%, which implies a moderate contrast sensitivity (Mäthger et al., 2006). Taken together, these indicate that substrate contrast is an important visual cue for cuttlefish to modulate their body patterns.

4.2. Visual perception and camouflage

Although it has been long argued that disruptive coloration works by a different mechanism than background matching to achieve camouflage (Cott, 1940, Edmunds, 1974; Thayer, 1909), few empirical examples exist to support this notion (Stevens, Cuthill, Alejandro Parraga et al., 2006). Accumulated evidence in a variety of species supports the concept that disruptive body patterning may be distinctly different from background matching (Cuthill, Stevens, Windsor, & Walker, 2006; Cuthill et al., 2005; Fraser et al., 2007; Merilaita, 1998; Merilaita & Lind, 2005; Schaefer & Stobbe, 2006; Stevens & Merilaita, 2009b; Stevens, Cuthill, Windsor et al., 2006). However, to understand the principles of these two camouflage tactics, it is necessary to consider visual perception of the predators, i.e., the eyes of the beholder (Guilford and Dawkins, 1991; Stevens, 2007; Troscianko, Benton, Lovell, Tolhurst, & Pizlo, 2009). While cuttlefish disruptive body patterns in some cases represent a random sample of the background, which is in accordance with one aspect of the definition of background matching, the significance of disruptive coloration is the presence of strongly contrasting elements that break up the body outline. It is this effect of false edges that exploits the predator's edge and line detection mechanisms in early visual processing (Stevens and Cuthill, 2006; Troscianko et al., 2009). Furthermore, object recognition in high-level vision usually requires a figure-ground segregation, in which figure (or object) must be reliably differentiated from ground (or background) before object perception occurs (Bruce, Green, & Georgeson, 2003). These contrasting elements in disruptive coloration provide salient visual cues for figure-ground segregation, thus the predators might tend to treat individual disruptive components as objects rather than the animal as a whole. From the

visual perception of the predators, disruptive coloration is fundamentally different from background matching.

Acknowledgments

We are grateful to the Sholley Foundation for partial support of this project. We also thank Lydia Mäthger and Alexandra Barbosa for valuable discussions. CCC was supported by the MBL summer research fellowship. Special thanks to the Animal Care Staff of the Marine Resources Center of the MBL.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2009.04.002.

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